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The plankton communities from peat bog pools: structure, temporal variation and environmental factors

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This is the first characterization of the structure and temporal variation of the plankton communities comprising the complete food web in five peat bog pools related to environmental factors over two consecutive ice-free periods in Tierra del Fuego (54°S). Remarkably, picophytoplankton was composed solely of eukaryotic cells, surpassing the dominance expectations for these acidic water bodies, whereas testaceans were virtually absent, even as tychoplankters. Abundances of the different planktonic communities were slightly higher than those reported for Northern Hemisphere peat bogs and humic lakes. Mixotrophic nutrition prevailed among nano- and microphytoplankters, a strategy also common in humic lakes. The structures in spring of the planktonic communities were similar. In contrast, in late summer there were differences in the abundance and biomass of the different trophic compartments among small, shallow water bodies and large ones. These seem to be dictated by distinct pool size-driven patterns of water temperature variation. A general shift in the control of heterotrophic flagellates abundance in the pools occurred, changing from bottom-up regulation in spring to top-down control in late summer related to

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temperature-dependant variations in zooplankton abundance and composition. We hypothesize that changes in the trophic interactions affecting the entire food web occur over the open water period in these aquatic ecosystems, and that these are dictated by pool morphometry and related abiotic features.

KEYWORDS: peat bogs; food web; pools; plankton; Tierra del Fuego

INTRODUCTION

Peatlands are a wetland type widely distributed globally, characterized by the capacity of accumulating dead organic matter (peat), coming in most cases from slowly decomposing *Sphagnum* spp. mosses. Their development is strongly related to topography, and also requires particular environmental conditions leading to permanent waterlogging, i.e. low temperatures, high humidity and abundant, evenly distributed precipitation, met at high latitudes (Roig and Roig, 2004) or altitudes, in South America mostly along the Andes (McQueen, 1995; Cooper *et al.*, 2010). The accumulation of peat modifies the environment, causing a progressive decrease in pH, conductivity and nutrient concentrations. This is partly due to the high cation exchange capacity of *Sphagnum* spp., which takes up base cations and liberates protons (Clymo, 1964). The upward development of peat finally results in a dome-shaped area isolated from ground water called a peat bog (Roig and Roig, 2004). This system usually contains several pools which retain most of the water input due to precipitation, thus acting as water flow regulators (Iturraspe, 2010). Individual pools in the same peat bog can show distinct chemical features, even when only a few meters apart (Mataloni and Tell, 1996). Pools interconnected by natural surface channels collect water from sources other than direct rainfall, and show higher values of pH and hardness, minerotrophic status (González Garraza *et al.*, 2012). However, as *Sphagnum* spp. mosses surrounding the pools grow upward, these become hydrologically isolated, fed only by precipitation and their waters turn softer and more acidic, ombrotrophic status (Rydin and Jeglum, 2006; Iturraspe, 2010; González Garraza *et al.*, 2012).

Pools contain large amounts of dissolved organic carbon (DOC), mostly derived from moss decomposition (Rydin and Jeglum, 2006). Jones (Jones, 1992) suggested that the microbial loop in these humic pools could play an important role in channelling energy from allochthonous carbon inputs to metazoans, rather than recycling dissolved organic matter that leaks from the grazing food chain; thus the food web could be largely sustained by bacterial production (Rydin and Jeglum, 2006). However, microbial communities inhabiting peat bog pools have been poorly studied (Gilbert and Mitchell, 2006). Previous studies around the world have surveyed only partially the plankton food web in these shallow limnetic systems (Sharma and Bhattarai, 2005; Druvietis *et al.*, 2010), which in theoretical terms have been placed within the more general category of "humic" water bodies. In fact, knowledge about humic environments is mostly based on studies of Northern Hemisphere humic lakes (Keskitalo and Eloranta, 1999), which show completely different hydrological and morphometric characteristics than the shallow water bodies from peat bogs. Therefore, the study of the latter and their plankton communities should expand our knowledge about humic aquatic ecosystems.

While most peatlands are located in the Northern Hemisphere, Tierra del Fuego Island encompasses the southernmost area of extensive peat bog development (Lindsay *et al.*, 1988). Within this area, Mataloni and Tell (Mataloni and Tell, 1996) carried out the first ecological study of the phytoplankton in Rancho Hambre peat bog. These authors found that shallow pools differed from deep ones in their algal species composition, and that a number of abiotic variables [pH, conductivity and dissolved reactive phosphorus (DRP)] were strongly correlated to the relative frequencies of some major taxonomic groups. Thus environmental diversity appeared to be crucial for the structure and composition of the phytoplankton inhabiting these water bodies. In turn, shallow lakes and pools from the neighbouring Antarctic Peninsula proved to be dynamic environments in which temperature-driven changes in abiotic features over the ice-free season largely dictated the structure of planktonic communities over a trophic gradient (Izaguirre *et al.*, 2003) as well as the regulation of phytoplankton abundance (Mataloni *et al.*, 2000). The present study aims at characterizing the plankton communities (from bacterioplankton up to zooplankton) over two seasonal cycles in five pools with different morphometric and abiotic conditions, under the hypotheses that: (i) environmental factors distinctly influence the structure of the plankton communities inhabiting pools of different morphometric features from Rancho Hambre peat bog; and (ii) temperature-driven seasonal changes of such environmental variables in turn impose changes on the interactions among plankton communities.

METHOD

Study sites

Rancho Hambre peat bog is located ~50 km from Ushuaia city, within the southernmost main watershed of Tierra del Fuego Island, Argentina (Iturraspe and Urciuolo, 2000). The area is cold-temperate; monthly mean air temperature and monthly mean precipitation values recorded over the study period were 4.1°C and 60 mm, respectively (González Garraza *et al.*, 2012). The central area of Rancho Hambre has a characteristic dome shape, and the vegetation is dominated by the moss *Sphagnum magellanicum* Bridel. Five pools, located on a transect across the peat bog, were selected to represent the two common sets of morphometric features of these water bodies, as described by González Garraza *et al.* (González Garraza *et al.*, 2012). RH1, RH2 and RH4 were relatively large and deep (average maximum depth 132 cm), of which RH4 was the largest water body in Rancho Hambre; while RH3 and RH5 were small and shallow (average maximum depth 33 cm) (Fig. 1 and Table I).

Sampling regime, physicochemical analyses

All pools were sampled on eight occasions during two consecutive seasonal cycles during the ice-free period, between October 2008 and April 2010. According to their size, one to four sampling sites were selected within each pool. Three sampling points (shore, limnetic surface and bottom) were established in RH1 and RH2, and four points (north and south shores, limnetic surface and bottom) in RH4. Sampling of the limnetic bottom point was performed using a 5-L Van Dorn bottle. RH3 and RH5 were only sampled from the shore. The geographic position of the sites was determined using a GPS (Garmin, USA). Temperature, pH and conductivity were measured *in situ* with a multiparametric probe (HORIBA, Japan). The concentrations of Ca^{2+} and Mg^{2+} as $CaCO_3$ (mg L^{-1}) were determined separately from unfiltered samples according to the calmagite colourimetric method, using a Hach DR2800 spectrophotometer (Hach Company, USA) and its corresponding reagent kit. Total hardness (TH) as mg equivalent $CaCO_3$ L^{-1} was calculated on the basis of these determinations according to the standard method 2340C (APHA, 1995). Samples for dissolved nutrient analyses were filtered through 0.7-μm-pore size Millipore APFF prefilters (Millipore Corporation, USA). Concentrations of ammonium, nitrate + nitrite and DRP were determined from the filtrates according to the salicylate, cadmium reduction-diazotization and ascorbic acid methods respectively, using a Hach DR2800 spectrophotometer (Hach Company, USA) and their corresponding reagent kits. Dissolved inorganic nitrogen (DIN) was calculated as the sum of ammonium plus nitrate + nitrite concentrations. DOC was determined from filtered water with the high temperature Pt catalyst oxidation method (Shimadzu analyzer TOC-5000A, SM 5310B technique)

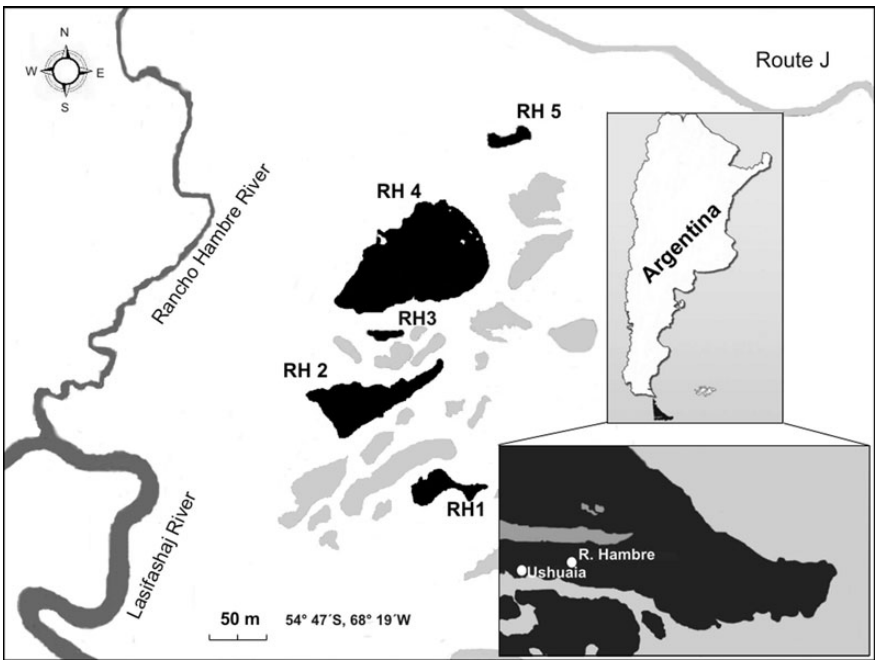

Fig. 1. Map of Rancho Hambre peat bog. Pools studied are in black (after González Garraza *et al.*, 2012).

Table I: Main morphometric and physicochemical features of the five pools from Rancho Hambre peat bog (Tierra del Fuego)

Pool	RH 1	RH 2	RH 3	RH 4	RH 5
Latitude (S)	54° 44′ 52.87″	54° 44′ 48.61″	54° 44′ 46.75″	54° 44′ 41.51″	54° 44′ 39.35″
Longitude (W)	67° 49′ 29.44″	67° 49′ 31.66″	67° 49′ 32.21″	67° 49′ 31.69″	67° 49′ 26.7″
Surface area (m^2)	1824	5976	137	16,190	542
Maximum depth (cm)	95	150	33	150	33
Temperature (°C)	8.8 (2.3–17.5)	8.6 (1.1–15.9)	11.8 (3.2–24.9)	8.5 (3.3–14.9)	10.6 (1.7–19.7)
pH	5.7 (5.0–7.1)	4.5 (3.8–5.5)	4.5 (3.6–5.4)	6.3 (5.2–7.0)	4.6 (4.1–5.4)
Conductivity ($\mu S\ cm^{-1}$)	24 (14–50)	23 (9–40)	33 (10–82)	30 (16–60)	26 (5–50)
TH (mg equivalent $CaCO_3\ L^{-1}$)	26 (7–41)	24 (7–46)	22 (8–43)	30 (11–43)	22 (11–36)
DIN (μM)	3.3 (0.5–7.3)	3.8 (0.5–17.1)	3.9 (0.7–7.4)	3.1 (1.4–7.6)	2.6 (0.0–5.2)
DRP (μM)	1.7 (0.8–2.7)	1.5 (0.7–2.5)	2.0 (1.0–4.2)	1.1 (0.5–1.9)	1.0 (0.6–1.6)
DOC (mM)	0.65 (0.45–0.80)	0.64 (0.42–0.75)	0.93 (0.23–1.22)	0.43 (0.37–0.50)	0.77 (0.32–1.04)

Mean values are given, with minimum and maximum values in parentheses ($n = 8$ for each pond). TH, total hardness ($Ca^{2+} + Mg^{2+}$); DIN, dissolved inorganic nitrogen; DRP, dissolved reactive phosphorus; DOC, dissolved organic carbon.

following the recommendations of Sharp *et al.* (Sharp *et al.*, 1993). DOC was measured from April 2009 to the end of the study period.

Picoplankton and heterotrophic flagellates

Water samples were collected using 120-mL plastic flasks and fixed *in situ* with 2% glutaraldehyde. For picoplankton enumeration, subsamples (2–5 mL) were stained with 4.6 diamidino-2-phenylindole (DAPI, 5 $\mu g\ mL^{-1}$ final concentration) and filtered onto 0.22-μm-pore size black polycarbonate filters according to Porter and Feig (Porter and Feig, 1980). For heterotrophic flagellates (HF) enumeration, subsamples (8–25 mL) were stained with DAPI as described above and filtered through 0.8-μm-pore size black polycarbonate filters. Filters were inspected by epifluorescence microscopy using an Olympus BX40F4 (Olympus, Japan) at ×1000 magnification. Heterotrophic bacteria (HB) were enumerated under UV light excitation; picocyanobacteria under blue and green light excitation; picoeukaryotic algae (Peuk) under blue light excitation (Callieri and Pinolini, 1995), and HF under blue and UV light excitation. Random fields were counted until an error <20% in the estimation of abundance was obtained (Venrick, 1978). Cell size was estimated by image analysis following Massana *et al.* (Massana *et al.*, 1997) for HB, while cell shape was approximated to geometrical figures according to Hillebrand *et al.* (Hillebrand *et al.*, 1999) for Peuk and HF. The carbon to volume relationship derived by Norland (Norland, 1993) from the data of Simon and Azam (Simon and Azam, 1989) was used to calculate HB biomass; whereas the carbon-conversion factors according to Søndergaard *et al.* (Søndergaard *et al.*, 1991) and Børsheim and Bratbak (Børsheim and Bratbak, 1987) were used for Peuk and HF, respectively.

Nano- and microphytoplankton

Concentrated phytoplankton samples for qualitative analysis were taken by diagonally towing an 18-μm mesh size net in the limnetic zone in deep pools, and by bucket scooping ca. 50 L of water and then filtering through the same net in shallow ones so as to avoid disturbing the loose bottom sediment. One subsample was observed *in vivo*, and the other preserved in 4% formalin for identification of microalgae. Identifications were made using the taxonomic literature (West and West, 1904, 1905, 1908, 1912, 1922; Irénée-Marie, 1939; Cosandey, 1964; Komárek and Fott, 1983; Krammer and Lange-Bertalot, 1986, 1988, 1991; Komárek and Anagnostidis, 1999, 2005) as well as previous surveys of the microalgal flora of Tierra del Fuego peat bogs (Mataloni, 1991, 1995a, 1995b, 1997). Two replicate samples for quantitative analyses of the nano- and micro-sized fractions were collected using 120-mL plastic flasks and preserved with 1% acetic Lugol's solution. Replicate 10-mL plankton chambers were left to sediment for at least 24 h and counts performed in an inverted microscope at ×400 magnification according to Utermöhl (Utermöhl, 1958). A maximum counting error of 20% was accepted in estimating the abundance of the dominant taxa (Venrick, 1978). Mean cell volumes of the phytoplankton were estimated by approximating cell shape to geometrical figures following Hillebrand *et al.* (Hillebrand *et al.*, 1999), and converted to biomass using the carbon-conversion factors given by Reynolds (Reynolds, 2006). Nano- and microphytoplankters were classified into two trophic categories: autotrophic phytoplankton (AP) and mixotrophic flagellates (MF). The latter comprised those pigmented species or groups of taxa for which phagotrophy has already been documented, among them *Ochromonas* spp. (Boëchat *et al.*, 2007), *Dinobryon sertularia* (Bird and Kalff, 1987), dinoflagellates

(Loeblich, 1984), *Cryptomonas* spp. (Urabe *et al.*, 2000; Danilov and Ekelund, 2001; Lepistö and Holopainen, 2003) and *Dictyochophyceae* (Unrein *et al.*, 2005).

Ciliates

Ciliates were sampled with a wide-mouth 1 L bottle and fixed *in situ* with 2% acetic Lugol's solution (Finlay and Guhl, 1992). After settling for 24 h, each sample was concentrated into 120 mL. Live samples were also obtained and preserved in the cold in order to establish laboratory cultures. Species identifications were made after performing silver impregnations with protargol according to Wilbert (Wilbert, 1975), along with live observations under stereo- and bright-field microscopes. Classification followed Lynn (Lynn, 2008) and species identifications were made according to Kahl (Kahl, 1930, 1931, 1932, 1935), Foissner *et al.* (Foissner *et al.*, 1991, 1992, 1994, 1995, 1999), Foissner and Berger (Foissner and Berger, 1996), and specific taxonomic papers. Two replicate quantitative samples per sampling location were allowed to settle for 24 h and counted under the inverted microscope at ×150 and ×600 magnifications by scanning the entire bottom of a 10-mL chamber (Utermöhl, 1958). Most abundant ciliates were enumerated separately, while less abundant ones were grouped together. Ciliate volumes were determined approximating the shape of Lugol fixed cells to geometrical figures (Hillebrand *et al.*, 1999), applying the correction of Müller and Geller (Müller and Geller, 1993). The carbon-conversion factor according to Putt and Stoecker (Putt and Stoecker, 1989) was used to estimate biomass.

Testaceans

As testaceans are known to be abundant in the interstitial water among *Sphagnum* plants, but not in the pool water, at each site duplicate quantitative samples were taken only from the shore by filtering 35 L of water through a 15-μm-pore net and fixing the concentrated sample with 1% acetic Lugol's solution (Finlay and Guhl, 1992). Replicate 10 mL plankton chambers were left to sediment for at least 24 h and counts performed in an inverted microscope at ×400 magnification according to Utermöhl (Utermöhl, 1958).

Metazooplankton

Concentrated qualitative samples were collected in the limnetic zone by diagonally towing a 110 μm-mesh size net for mesozooplankton (cladocerans, adult copepods and copepodites) and a 53 μm-mesh size net for microzooplankton (copepod nauplii and rotifers) in deep pools, and by bucket scooping ca. 50 L of water and then filtering them through the same nets in shallow ones so as to avoid disturbing the loose bottom sediment. Samples were fixed *in situ* with 96% ethanol. Duplicate quantitative samples were taken with a 5-L Van Dorn bottle; 5 to 20 L water samples were filtered through a 53 μm-mesh sieve and fixed *in situ* with 4% formaldehyde. Mesozooplankton was subsampled with a Russell device and counted in a 5-mL Bogorov counting chamber using a stereomicroscope. Microzooplankton was subsampled with a Hensen Stempel pipette and counted in a 1-mL Sedgewick-Rafter counting cell using a compound microscope. At least three subsamples were analysed per sample or as many as necessary to get a counting error below 10% (José de Paggi and Paggi, 1995). Taxonomic identifications basically follow Reid (Reid, 1985) and Bayly (Bayly, 1992) for copepods; Paggi (Paggi, 1979, 1995), Smirnov (Smirnov, 1992), Orlova-Bienkowskaja (Orlova-Bienkowskaja, 1998) and Benzie (Benzie, 2005) for cladocerans; and Ruttner-Kolisko (Ruttner-Kolisko, 1974), Boltovskoy and Urrejola (Boltovskoy and Urrejola, 1977) and Voigt and Koste (Voigt and Koste, 1978) for rotifers. Rotifer volumes were estimated by applying geometric formulas according to Ruttner-Kolisko (Ruttner-Kolisko, 1977), and transformed to dry weight following Dumont *et al.* (Dumont *et al.*, 1975). Dry weight of cladocerans and copepods was calculated according to Bottrell *et al.* (Bottrell *et al.*, 1976). Biomass of metazooplankton as carbon content was estimated as 48% of their dry weight (Andersen and Hessen, 1991; Rossa *et al.*, 2007). Metazooplankters were divided into the following five "taxonomic-trophic" groups: micro-filter feeding rotifers (MFR), micro-filter feeding nauplii (MFN), filter feeding cladocerans (FC), omnivorous copepods (OC) and predators (P, comprising adult cyclopoid copepods and rotifers). Among rotifers, raptorial ones were classified as predators, whereas other rotifers including some algae graspers were grouped as MFR.

Empirical model

The Gasol model (Gasol, 1994) allows assessment of the importance of top-down vs. bottom-up mechanisms in controlling the abundance of HF based on a large database which included freshwater bodies over a wide range of trophic states. The model consists of a bivariate space where the (log)- transformed HB and HF abundances are plotted. A "maximum attainable abundance line" (MAA) is computed depicting the HF abundance that can be attained for a given HB abundance, assuming HF to feed only on HB; and also a "mean realized abundance line" (MRA) based on the observation that MAA of HF is rarely reached in natural systems. The location of data points below the MRA line indicates that the abundance

of HF is mainly driven by top-down control, while samples located closer to the MAA line suggest bottom-up regulation. Distance (D) for any given system is calculated as the difference between the actual HF abundance and the maximum predicted by the MAA line for the HB abundance recorded. This parameter reflects the degree of uncoupling between HF and HB, and correlates to the abundance of potential HF predators (Gasol, 1994).

Data analyses

For each large pool, randomized complete block multivariate analyses of variance employing sampling dates as blocks and sites of the pool as fixed effects factors, as well as individual randomized block model III two-factor analyses of variance without within-cell replication for each abiotic variable did not show significant differences between sampling points (Zar, 2010). Therefore, sampling points within each large pool were considered as grab samples of a composite sample of the pool, and values of all variables averaged per sampling date.

A principal component analysis (PCA) based on the abundance matrix of plankton communities was performed to characterize pools according to their trophic web composition, by means of the software NTSYSpc 2.2 (Exeter Software, USA). The abundance data were ($\log_{10} + 1$) transformed prior to the PCA analysis (ter Braak and Smilauer, 2002). Spearman's rho was used to estimate correlation between all variables, using the SPSS 15.0.1 software (StatSoft, USA).

RESULTS

Abiotic conditions

Field observations showed that of the three large water bodies, only RH1 and RH4 had inflows and/or outflows (i.e. natural surface channels), while RH2 as well as shallow RH3 and RH5, did not. Mean water temperatures of the five pools over the eight sampling occasions varied between 8.5 and 11.8°C, with an overall variation range of 1.1−24.9°C (Table I). Large water bodies (RH1, RH2, RH4) had both lower average temperatures and narrower ranges than small, shallow ones (RH3, RH5). pH varied little over time, and clustered the pools into two groups: mildly acid (RH1 and RH4, mean pH = 6, range 5.0−7.1) and acid ones (RH2, RH3 and RH5, mean pH = 4.5, range 3.8−5.5).

Concentrations of dissolved nutrients in all the water bodies were within the same range; thus, temporal fluctuations within each of them exceeded the spatial variation across the whole set at any given sampling (Table I). An exhaustive analysis of the abiotic characteristics from these pools can be found in González Garraza *et al.* (González Garraza *et al.*, 2012).

Abundance and composition of plankton communities

HB mean abundance over the study period in each pool was between 6.2 and 11.1 × 10^6 cells mL^{-1} (Fig. 2a). On account of temporal variation of abundance within each annual cycle, lowest values were recorded in spring (October) in all pools (<3.8 × 10^6 cells mL^{-1}), while highest ones were generally observed in summer (December and February), up to 2.8 × 10^7 cells mL^{-1}. HB abundance was significantly correlated with temperature ($r = 0.34$, $P = 0.031$, $n = 40$), and no filamentous morphotypes were observed throughout the study.

Noticeably, autotrophic picoplankton in all pools was composed solely of picoeukaryotes (Peuk). Their mean abundance varied from 3.3 to 9.3 × 10^3 cells mL^{-1} in all water bodies but RH2 (Fig. 2b), which showed a mean value of 5.1 × 10^4 cells mL^{-1}, with peaks in February and April (up to 1.9 × 10^5 cells mL^{-1}).

Almost every HF in the pools was <5 μm in size and no general seasonal pattern was found regarding their abundance. Mean values over the study period in each pool ranged between 2.2 and 8.7 × 10^3 cells mL^{-1} (Fig. 3a). Abundance peaks in December and April, respectively, accounted for the higher mean abundances recorded in the small pools RH3 and RH5.

Abundance of nano- and microphytoplankton (>2 μm size fraction) was significantly correlated with temperature in all pools ($r = 0.52$, $P = 0.001$, $n = 40$), with lowest values in spring and highest in summer in most pools over the two seasonal cycles (Fig. 3b). This size fraction was generally dominated by MF in all pools. This group mostly comprised chrysophytes, among which *Ochromonas* spp. were the most abundant, and averaged 70% of the total nano-microphytoplankton abundance. However, peaks of AP species were observed in December in the different pools, mainly the flagellated Cryptophyte *Plagioselmis* sp. and the Chlorococcalean *Kirchneriella microscopica* Nygaard (González Garraza, 2012). The ratio MF:HF was generally >1 in all pools in February, indicating that mixotrophs dominated among flagellated grazers. During the rest of the open water period, MF dominated in RH1 and HF in RH4, while the mean MF:HF was ~1 in the other pools. In all, mixotrophy dominated among nano-microplankters (AP + MF + HF), since on average 42% of the total nano-microplankton were MF, 38% HF and 20% AP when considering all pools and dates together.

Ciliate dominant taxa and their feeding habits are shown in Table II; and their abundances during the

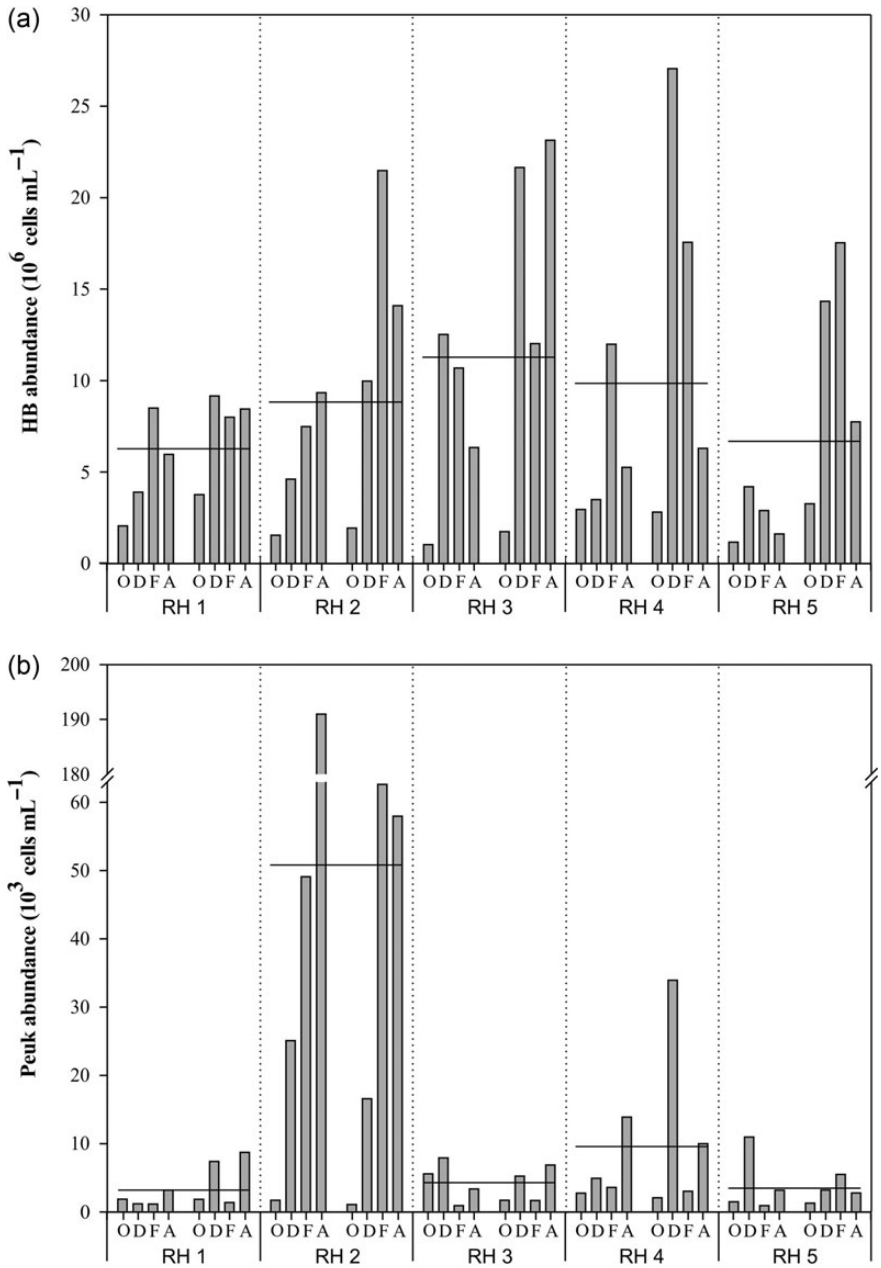

Fig. 2. Abundances of (**a**) heterotrophic bacteria (HB) and (**b**) picoeukariotic algae (Peuk) in the pools studied. Bars indicate mean values over the study period for each water body.

study period in Fig. 4. Mixotrophic species were observed only in low abundances in Rancho Hambre, and were thus pooled with less abundant ciliates as "other ciliates". As to annual trends, total abundance peaked in autumn (April) in large RH1 and RH4. Remarkably, raptorial feeders such as *Balanion planctonicum* (Foissner, Oleksiv and Müller) Foissner, Berger and Kohmann and *Urotricha* spp. dominated the spring and autumn samples (October and April); except in pools RH2 and RH5, where the highly efficient fine suspension feeders *Rimostrombidium hyalimun* (Mirabdullaev) Petz and Foissner and *Cyclidium* sp., respectively, were occasionally dominant. In turn, *Pelagostrombidium fallax* (Zacharias) Krainer was the largest among the dominant taxa, and was present in all pools with higher abundances in summer. Regarding testaceans, only a few dead specimens ($\sim$1 ind. L^{-1}) were

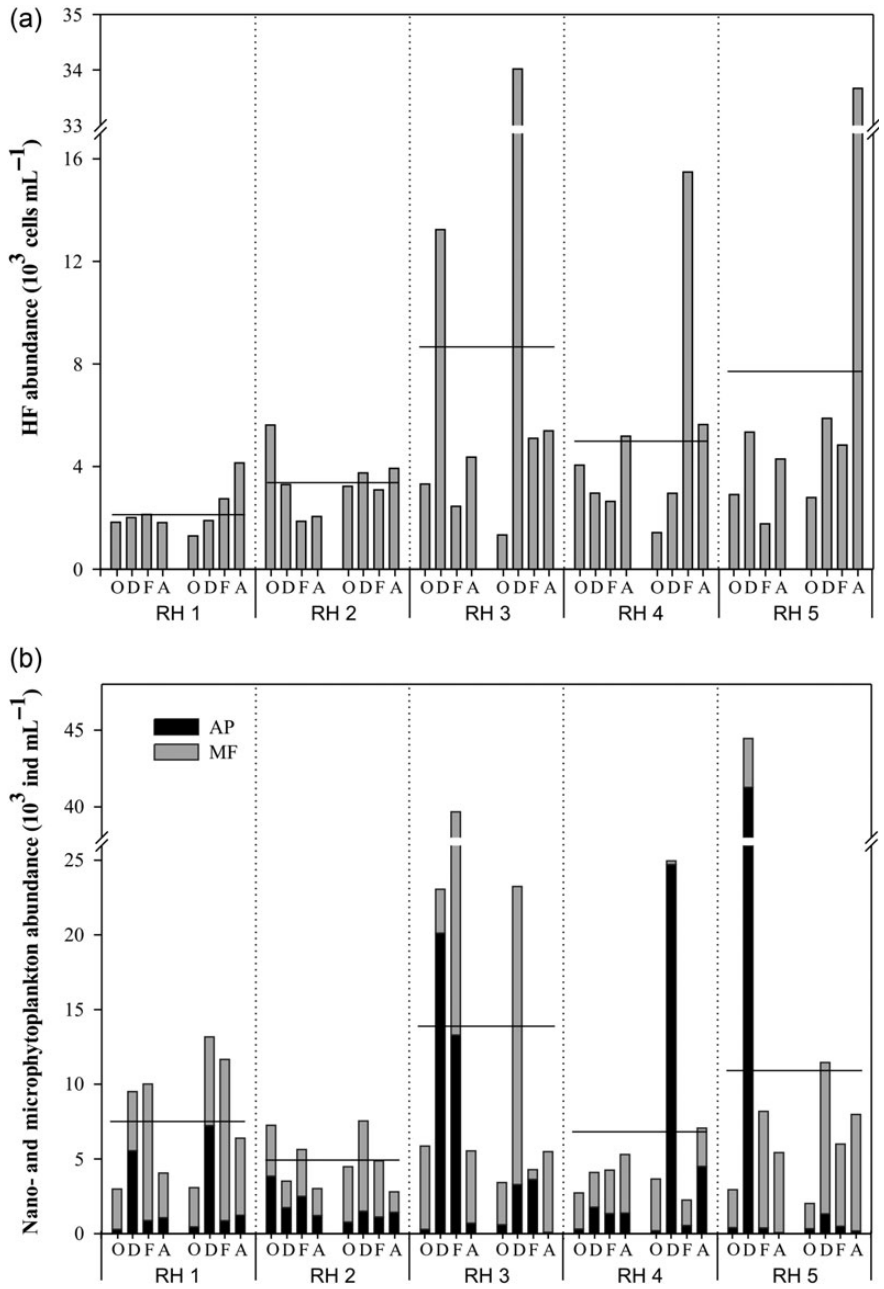

Fig. 3. Abundances of (**a**) heterotrophic flagellates (HF) and (**b**) nano- and microphytoplankton in the pools studied. AP, autotrophic phytoplankton; MF, mixotrophic flagellates. Bars indicate mean values of total abundance over the study period for each water body.

found in the shore plankton samples. Only one living species (*Difflugia oblonga* Ehrenberg) was identified in RH5, also in very low abundances (up to 15 ind L^{-1}).

Dominant Metazooplankton taxa and their feeding habits are shown in Table III, and their total abundances in Fig. 5a. Metazooplankton total abundance was significantly correlated with temperature ($r = 0.55$, $P = 0.0002$, $n = 40$), lowest values were recorded in spring in all pools (<62 ind L^{-1}), and maximum values were recorded in February and April in the smallest ones (up to 6762 ind L^{-1}). Regarding the relative abundances of the five "taxonomic-trophic" groups, MFN accounted for over 70% of metazoan abundance in most October samples, whereas MFR dominated from December to April in most pools (Fig. 5b). Nevertheless, a distinct metazooplankton composition was observed in summer (December–February) in the largest pool RH4. Here, crustaceans dominated over rotifers, mostly due to FC.

Table II: Dominant ciliates from studied pools, and their feeding habits according to Šimek et al. (Šimek et al., 1996)

Taxa	Feeding habit	Cell size (μm^3)	Pool[a]
Oligotrichida			
Halteria grandinella (Müller) Dujardin	Highly efficient fine suspension feeders	8110	2
Pelagostrombidium fallax (Zacharias) Krainer	Less efficient fine suspension feeders, coarse filter feeders, detritophages	76,034	All
Rimostrombidium hyalinum[b] (Mirabdullaev) Petz and Foissner	Highly efficient fine suspension feeders	6719	2
Scuticociliatida			
Cyclidium sp.	Highly efficient fine suspension feeders	4465	5
Prostomatea			
Balanion planctonicum (Foissner, Oleksiv and Müller) Foissner, Berger and Kohmann	Raptorial feeders	575	1, 4
Large *Urotricha* sp.	Raptorial feeders	11,352	All
Small *Urotricha* sp.	Raptorial feeders	1441	All

[a]The pool/s with the highest abundances.
[b]Species feeding habit determined using species-specific grazing rates from Callieri *et al.* (Callieri *et al.*, 2002).

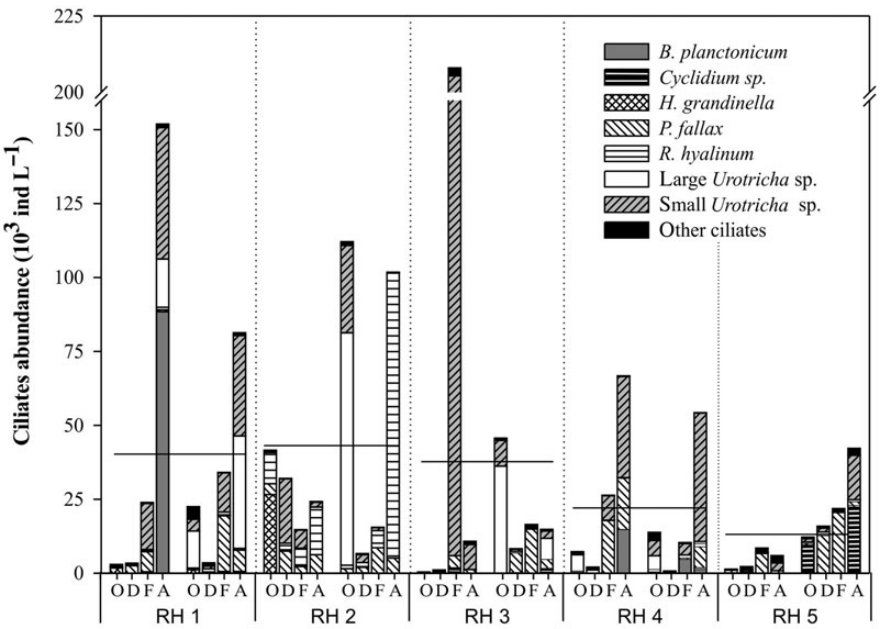

Fig. 4. Abundance and composition of ciliates in the pools studied. Bars indicate mean values of total abundance over the study period for each water body.

Structure of the plankton communities over the seasonal cycle

Results of the PCA based on the abundances of plankton communities in the five pools over the study period are shown in Fig. 6a and b in order to better display the eigenvectors representing the variables as well as the resulting ordination of samples. The first two axes accounted for 37.2% of the total variance. The first axis was positively associated with the abundances of FC, HB and MFR (eigenvectors 0.76, 0.71 and 0.69, respectively), and negatively with abundances of the ciliate *H. grandinella* and MFN (eigenvectors: −0.65 and −0.60, respectively) (Fig. 6a). In turn, the second axis was mostly influenced by the abundances of MF, Peuk and OC (eigenvectors: −0.64, 0.63 and 0.57, respectively). In Fig. 6b, ordination of samples along the first axis clearly shows the association of all spring (October) samples with high abundances of *H. grandinella*, MFN and large *Urotricha* sp., and low abundances of HB and adult metazooplankton. February and April samples from RH2 were in the upper right section of the diagram due to high Peuk, OC and AP abundances, while the same

Table III: Dominant metazooplankton taxa in the studied pools, and their feeding habits

Taxa	Feeding habit	Pool[a]
Rotifera		
Ascomorpha ecaudis Perty	Algae grasper	1, 3
Asplanchna girodi de Guerne	Predator	4
Colurella sp.	Micro-filter feeder	3, 5
Conochilus unicornis Rousselet	Micro-filter feeder	All
Keratella ona Boltovskoy and Urrejola	Micro-filter feeder	3, 5
Keratella valdiviensis Thomasson	Micro-filter feeder	2, 3, 5
Ploesoma truncatum Levander	Predator	3, 4, 5
Polyarthra dolichoptera Idelson	Algae grasper	All
Synchaeta pectinata Ehrenberg	Algae grasper	1, 4
Testudinella emarginula Stenroos	Micro-filter feeder	1, 2, 5
bdelloid rotifers	Micro-filter feeder	3, 5
Cladocera		
Alona spp.	Filter feeder	3, 5
Bosmina chilensis Daday	Filter feeder	All
Ceriodaphnia cf. *dubia* Richard	Filter feeder	1, 2, 4
Chydorus sp.	Filter feeder	3, 5
Daphnia commutata Ekman	Filter feeder	4
Pleuroxus sp.	Filter feeder	3, 5
Copepoda		
Boeckella poppei Mrázek		
Nauplii	Micro-filter feeder	All
Copepodites + adults	Omnivorous	All
Bryocyclops spp. (copepodites + adults)	Omnivorous	5
Diacyclops sp. (adults)	Predator	5
Eucyclops sp. (adults)	Predator	1
Harpacticoida Parastenocarididae (copepodites + adults)	Omnivorous	1, 4, 5
Tropocyclops prasinus meridionalis Kiefer		
Nauplii	Micro-filter feeder	2, 4, 5
Copepodites	Omnivorous	1, 2, 4
Adults	Predator	1, 2, 4

[a]The pool/s with high abundances.

sampling dates from small RH3 and RH5 are located in the lower right section of the diagram mostly due to high abundances of flagellates.

Figure 7 shows the abundance-based biomass of the plankton communities from Rancho Hambre pools in the two most distinct periods: spring (October) and late summer (February). As all pools showed similar plankton structures in spring (Fig. 6b), Fig. 7a is based on average values of the October samples from all five water bodies. On the other hand, metazoan abundance in February samples separated pools into two groups: large RH1, RH2 and RH4 (average 419 ind L^{-1}) and small RH3 and RH5 (average 2320 ind L^{-1}) (Figs. 5 and 6). Therefore, Fig. 7b and c are based on average values of the February samples for large and small pools, respectively. Regarding prokaryotes, although the biomass of HB increased from October to February in all pools, Peuk biomass increased more markedly in large ones due to the influence of RH2. The biomass of the nano- and microphytoplankton was equally represented by both nutritional strategies (MF and AP) in October. Yet, a clear dominance of the AP was observed in large pools in February, whereas small ones were dominated by MF. No clear changes in the biomass of HF and ciliates were observed between October and February, although ciliate species composition did change (Fig. 4). Metazoan taxonomic-trophic groups, in turn, displayed the most striking differences among the three models. In October, metazoan biomass was mostly composed of crustaceans (MFN, OC and FC). The latter two groups continued to dominate the metazooplankton from large pools in February, presumably contributed to by the recruitment of a large proportion of spring nauplii, which would also account for the increase in the predator biomass in these pools. However, in small pools it was the biomass of MFR which increased in February, hence largely dominating the metazooplankton.

Potential links between plankton communities

Figure 8a shows the positioning of all Rancho Hambre samples within the framework of the Gasol model (Gasol, 1994). According to it, HF abundance would be mostly bottom-up regulated in the five pools during the two consecutive seasons. Furthermore, distance D increased with

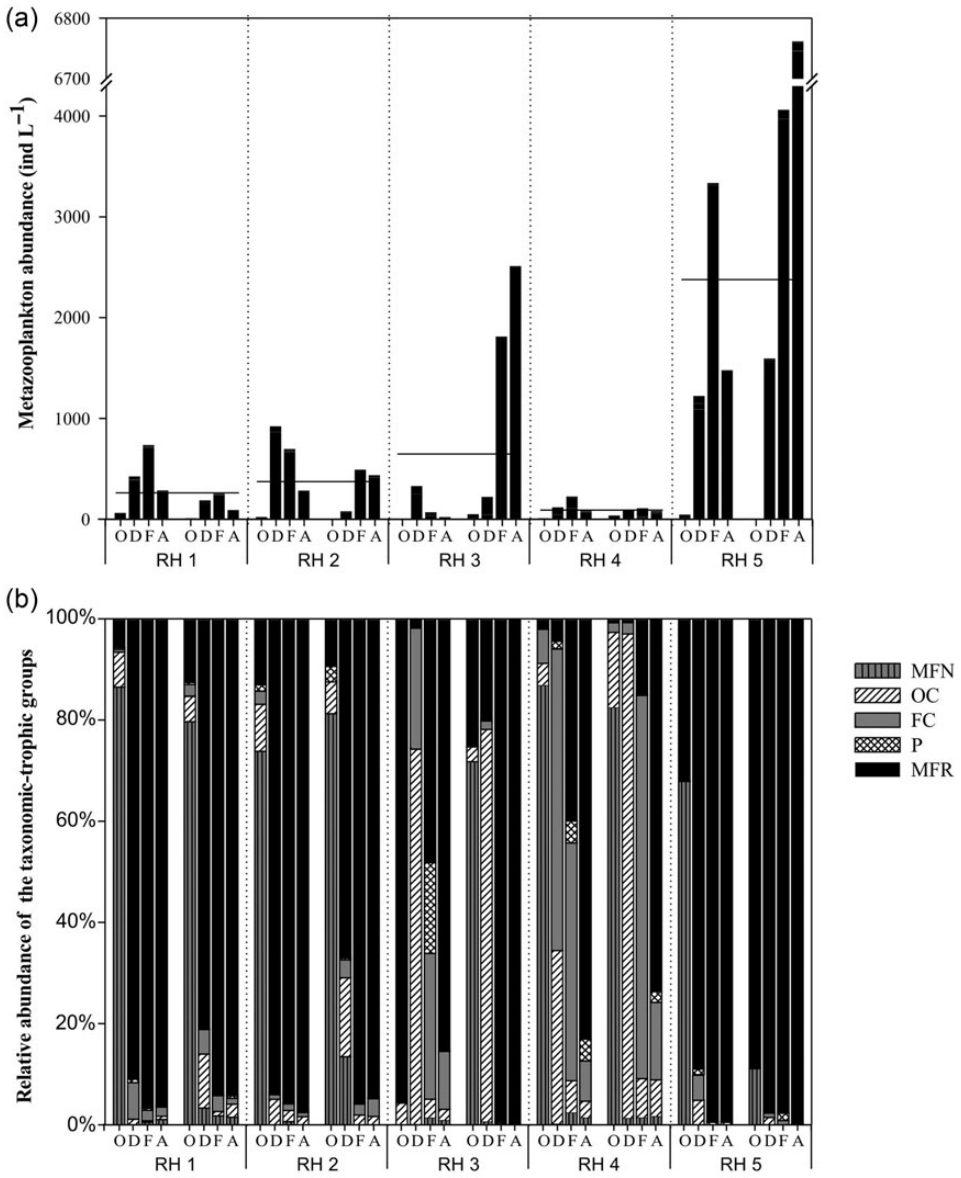

Fig. 5. (**a**) Total metazooplankton abundance, and (**b**) relative abundance of the five metazooplankton taxonomic-trophic groups in the pools studied. MFN, micro-filter feeding nauplii; OC, omnivorous copepods; FC, filter feeding cladocerans; P, predators; MFR, micro-filter feeding rotifers. Bars in (a) indicate mean values of total abundance over the study period for each water body.

increasing HB abundance in all pools, showing a highly significant correlation ($r = 0.64$, $P < 0.0001$, $n = 40$). Also, pooled data from spring (October) and late summer (February) samples were plotted in Fig. 8b. The positioning of samples suggests a general shift in the control of HF abundance, moving from bottom-up regulation in spring to top-down control in late summer. The mean abundance of HF varied slightly from 2.8×10^3 cells mL^{-1} (October) to 4.2×10^3 cells mL^{-1} (February), while HB mean abundance increased one order of magnitude, from 2.2×10^6 cells mL^{-1} (October) to 1.2×10^7 cells mL^{-1} (February). Calculated D for this group of samples was correlated with the abundances of FC, predators, OC, MFR and the large ciliate *P. fallax* ($r = 0.73$, $P < 0.001$; $r = 0.69$, $P < 0.001$; $r = 0.65$, $P = 0.002$; $r = 0.63$, $P = 0.003$; $r = 0.58$, $P = 0.008$; respectively, all $n = 20$).

DISCUSSION

Although peatlands occupy extensive areas in the Northern Hemisphere, information on the ecology of

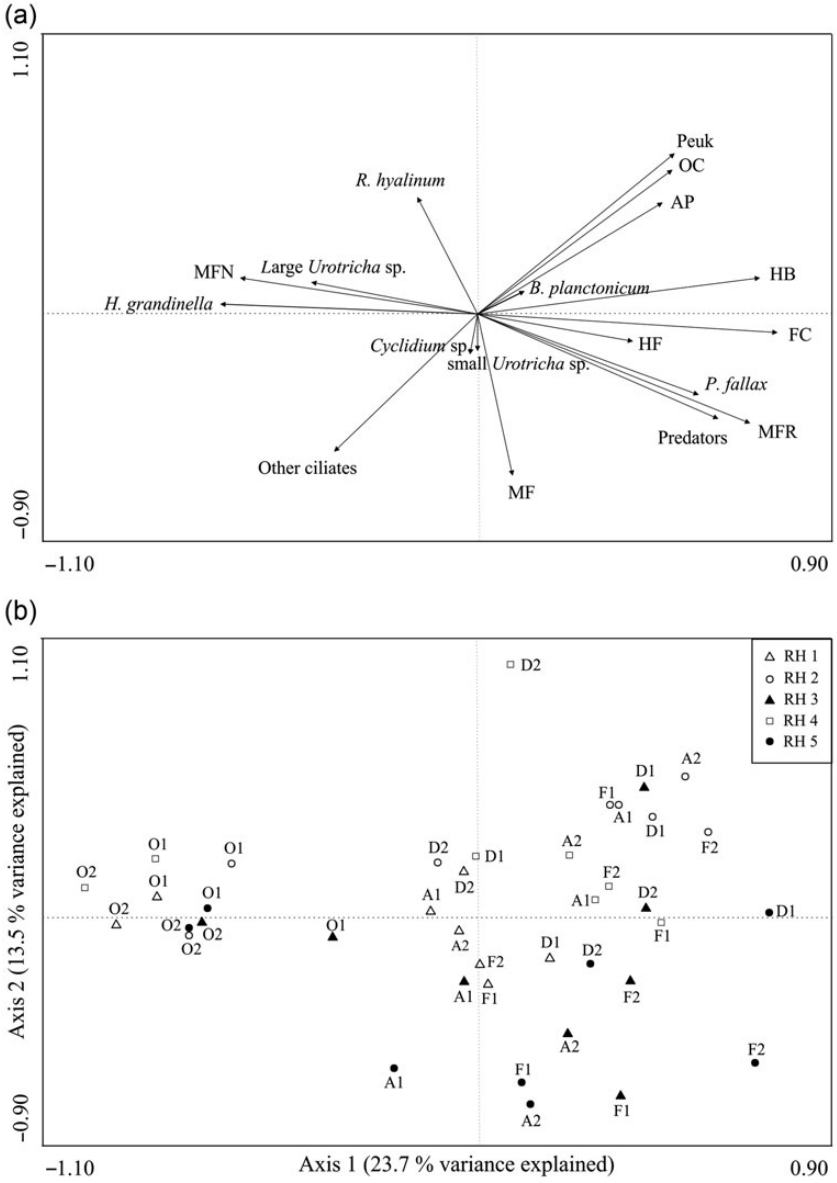

Fig. 6. Ordination plots obtained by Principal Component Analysis (PCA) based on the abundances of plankton communities. (**a**) Arrows indicate the loading of each variable on the two first axes. (**b**) Ordination of the samples based on these variables. HB, heterotrophic bacteria; Peuk, picoeukariotic algae; AP, autotrophic phytoplankton; HF, heterotrophic flagellates; MF, mixotrophic flagellates; MFR, micro-filter feeding rotifers; MFN, micro-filter feeding nauplii; OC, omnivorous copepods; FC, filter feeding cladocerans. Samples identification: letters indicate sampling month (O, October; D, December; F, February; A, April); numbers indicate sampling year (1, first; 2, second).

peat bog pools is rare (Gilbert and Mitchell, 2006; Rydin and Jeglum, 2006), and previous research has focused only on one or few plankton communities. As the present study represents the first survey of the complete plankton food web from peat bog pools, it is impossible to compare our results with other complex data sets from these environments.

Individual pools in the same peat bog can show very different chemical features, even when separated by only a few meters (Mataloni and Tell, 1996). According to González Garraza *et al.* (González Garraza *et al.*, 2012), the first axis of a PCA based on the abiotic features of these same samples represented a minero-ombrotrophic gradient along which RH1 and RH4 samples had high scores strongly associated with higher pH and TH values, while in the shallow ones (RH3 and RH5), fed only by precipitation, the water was softer and more acidic. In turn, RH2 shared features with both pool groups: on one hand it was relatively large and thus showed a similar temperature variation pattern to RH1

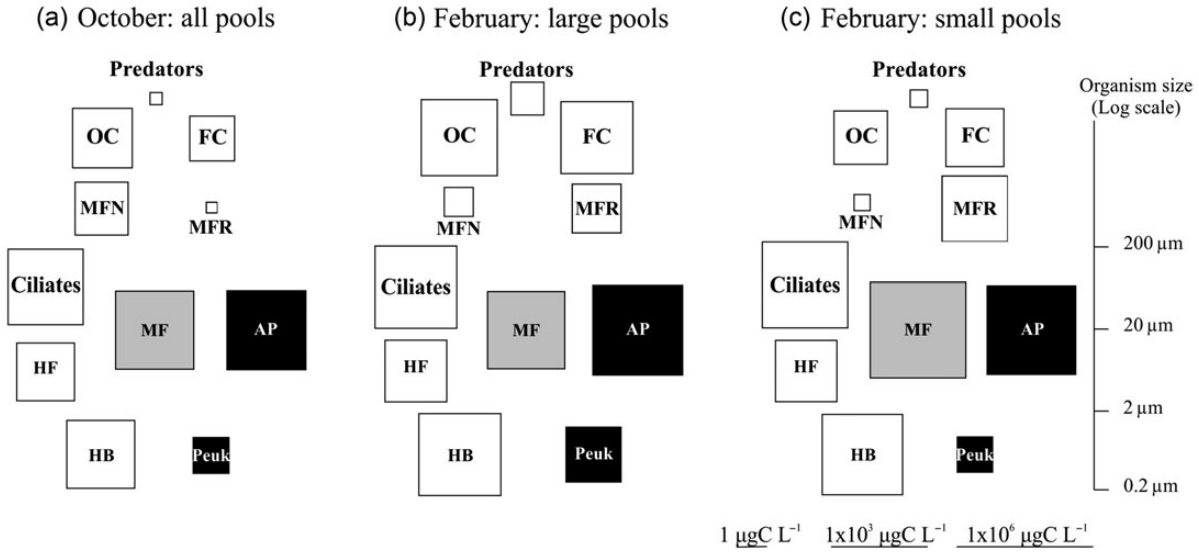

Fig. 7. Abundance-based biomass of the different plankton communities from Rancho Hambre pools in the two most distinct periods. (**a**) Averaged values for spring (October) samplings. (**b**) Averaged values for late summer (February) samplings from large pools (RH1, RH2, RH4). (**c**) Averaged values for late summer (February) samplings from small pools (RH3, RH5). Areas of the boxes are proportional to the biomass ($\log_{10}$ + 1-transformed) of the corresponding planktonic components. Abbreviations pertaining plankton communities as in Fig. 6. Nutrition mode: white, heterotrophic; grey, mixotrophic; black, autotrophic.

and RH4; on the other hand it was hydrologically isolated and shared ombrotrophic features with RH3 and RH5 (González Garraza *et al.*, 2012). Its particular features could partly explain the unique plankton structure found in RH2, where the abundance of Peuk was up to two orders of magnitude higher than in other pools, and picoplanktivorous ciliates as *H. grandinella* and *R. hyalunum* were observed in large abundances.

Mean abundances of HB in Rancho Hambre pools ($6.2–11.1 \times 10^6$ cells mL^{-1}) were slightly higher than the few records of average abundances available for peat bog pools: 1.39×10^6 cells mL^{-1} in a *Sphagnum* bog in Sweden (Langenheder *et al.*, 2006); 5.4×10^6 cells mL^{-1} in a raised bog in eastern Poland (Mieczan, 2010a); 1.2×10^5 cells mL^{-1} in the Jura Mountains of Switzerland (Lara *et al.*, 2011) and also for lakes within *Sphagnum* raised bogs in Latvia ($1.2–3.3 \times 10^6$ cells mL^{-1}) (Druvietis *et al.*, 2010). As regard to bacterial cell morphology, HB from these pools consisted mostly of small single cells. No grazing-resistant filamentous morphotypes exceeding 5 µm in length (Pernthaler *et al.*, 2004) were observed over the whole study, contrasting with extensive evidence of this survival strategy in oligo- to mesotrophic aquatic environments (Pernthaler *et al.*, 2004; Pernthaler, 2005). Pernthaler (Pernthaler, 2005) ascribed the absence of filamentous bacteria in oligotrophic oceanic waters to a particular interplay of resource limitation and predation. This explanation could also be valid for Rancho Hambre pools.

Nano- and microphytoplankton from Rancho Hambre was dominated by MF, mostly comprising the chrysophytes *Ochromonas* spp. These results agree with those of Lara *et al.* (Lara *et al.*, 2011), who found that chrysophytes were the most abundant sequences in the molecular analysis of the eukaryotic diversity from a peat bog pool. Mixotrophic nutrition is a successful strategy for algae under nutrient limiting conditions (Rothhaupt, 1996; Flöder *et al.*, 2006) especially in cold freshwater systems such as maritime Antarctic lakes where mixotrophic chrysophytes prevail during ice cover periods (Izaguirre *et al.*, 1998). Regarding ciliates, the mean abundances recorded in Rancho Hambre pools ($13.8–43.6 \times 10^3$ ind L^{-1}) were similar to those observed by Mieczan in different bog environments from eastern Poland: $7–26 \times 10^3$ ind L^{-1} for pools, $5–23 \times 10^3$ ind L^{-1} for peat ponds and $28–55 \times 10^3$ ind L^{-1} for small hollows (Mieczan, 2007a, b, 2010a). Furthermore, the autumn abundance peaks in pools RH1 and RH4 agreed with the seasonal dynamics described by Mieczan for ciliates in small water bodies from *Sphagnum* bogs (Mieczan, 2007a, b). Remarkably, only isolated individuals of testate amoebae were found in Rancho Hambre pools; in contrast to Mieczan (Mieczan, 2010a, b) who observed abundances of these protists $>2.1 \times 10^5$ ind L^{-1} in small hollows of raised bogs from eastern Poland. However, these small hollows (area 0.5–2 m^2, maximum depth 20 cm) receive a much stronger influence from the surrounding *Sphagnum* than the larger pools from Rancho Hambre (area 137–16,190 m^2,

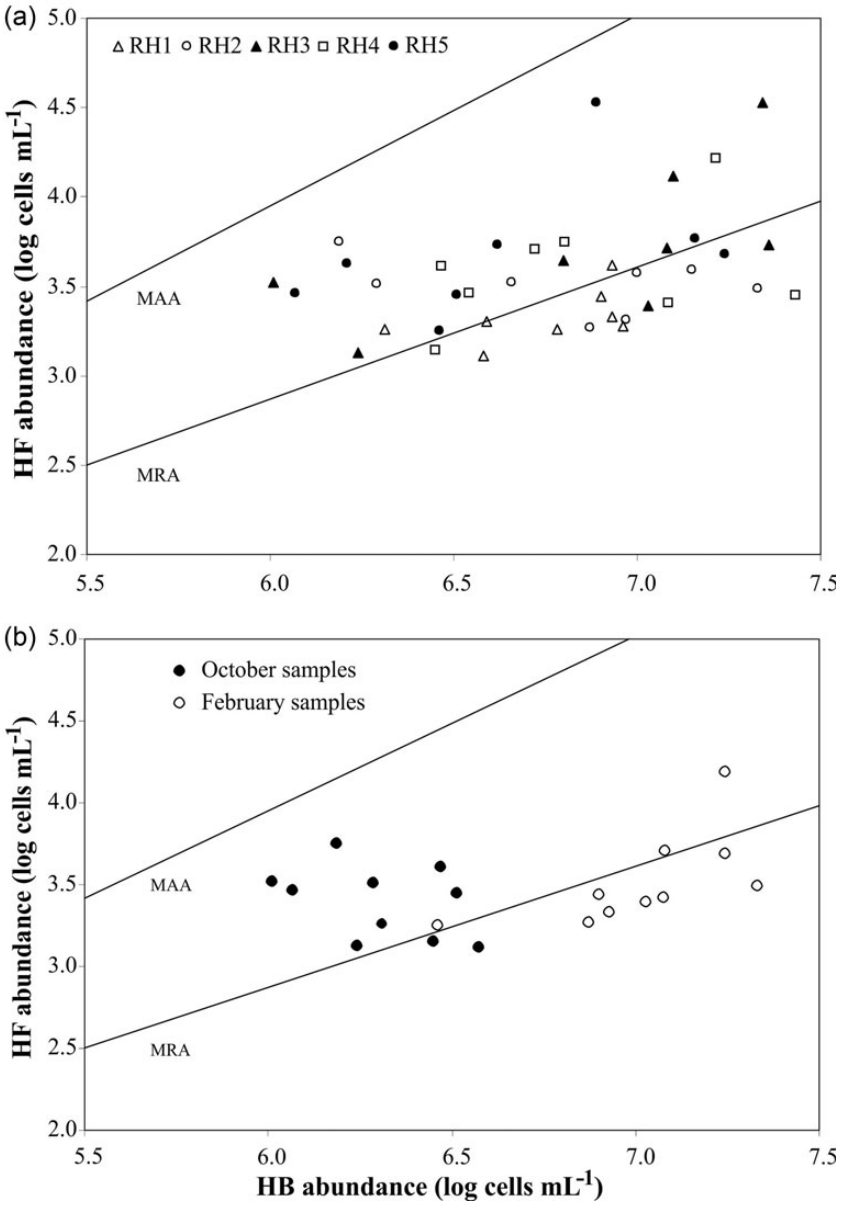

Fig. 8. Position of the samples within the framework of Gasol's model (Gasol, 1994). (**a**) All samples from the five pools. (**b**) Pooled October and February samples only. MAA, maximum attainable abundance line; MRA, mean realized abundance line.

maximum depth 33–150 cm). This is in line with Gilbert's (D. Gilbert, France, personal communication) opinion that the only living specimens found in this study in shallow RH5 would come from the sediment. Nevertheless, preliminary examination of *Sphagnum* samples from Rancho Hambre also revealed a very poor community composed of cosmopolitan species (D. Gilbert, France, personal communication). The surprising paucity of this group in Fuegian peat bogs deserves further biogeographical investigation.

Rancho Hambre metazooplankton was mostly dominated by MFR, with abundance peaks reaching 6762 ind L^{-1} (pool mean abundance over the study period 95–2313 ind L^{-1}). These results agree with those of Klimaszyk and Kuczynska-Kippen (Klimaszyk and Kuczynska-Kippen, 2006), who found that rotifers dominated over crustaceans in a peat bog pool from west central Poland, with abundance peaks of >8000 ind L^{-1}. In contrast, Sharma and Bhattarai (Sharma and Bhattarai, 2005) reported a maximum abundance of only

123 ind L^{-1} (range: 34–123 ind L^{-1}) with almost equal shares of Rotifera, Cladocera and Copepoda in a pond from a subtropical high altitude peat bog.

In all, the comparison of Rancho Hambre with the few previously studied bogs worldwide shows a similar composition of the dominant groups of phytoplankton and metazooplankton to high latitude peat bogs from the Northern Hemisphere, whereas abundances of the different plankton communities were similar or slightly higher to those previously reported in the literature. Nevertheless, further worldwide research is needed to determine whether this pattern could be generated by the scarcity of data for plankton communities from peat bog pools.

As peat bog pools are generally classified as humic water bodies (Keskitalo and Eloranta, 1999), it is assumed that their plankton structure would fit in the general characterization already obtained for other such environments. However, the abundances of HB, HF and nano-microphytoplankton found in Rancho Hambre pools were slightly higher than those reported for a bog lake in Wisconsin, USA (Graham *et al.*, 2004), the artificially divided bog lake Grosse Fuchskuhle in notheastern Germany (Macek *et al.*, 2001; Grossart *et al.*, 2008) and four humic lakes and a reservoir in Québec, Canada (Tadonléké *et al.*, 2005). Also, the maximum abundance of ciliates recorded during our study (2.1×10^5 ind L^{-1}) surpassed by one order of magnitude those reported for humic lakes by Graham *et al.* (Graham *et al.*, 2004) and Tadonléké *et al.* (Tadonléké *et al.*, 2005).

According to Callieri (Callieri, 2007), the abundance of eukaryotic picophytoplankton (Peuk) is generally one order of magnitude less than that of picocyanobacteria (Pcy); but in shallow, humic lakes the composition of picophytoplankton is quite unpredictable. Remarkably, we did not find any picocyanobacteria in any of Rancho Hambre pools during the two consecutive study seasons. These findings are in line with the results of Stockner and Shortreed (Stockner and Shortreed, 1991), who found that autotrophic picoplankton was dominated by Peuk in acidic humic lakes; and that numbers of picocyanobacteria decreased with decreasing pH, representing a negligible fraction of the total picophytoplankton below pH 6. Yet, the acidic character of Rancho Hambre pools could hardly explain the total absence of picocyanobacteria. As Callieri (Callieri, 2007) suggested that the "coloured organic waters" of such water bodies can favour bacterial growth, competition within the picoplanktonic size fraction could interact with pH to explain this fact.

Mixotrophic chrysophytes dominated not only the nano- and microphytoplankton fraction in Rancho Hambre, but were also numerically dominant over strictly HF. According to Bird and Kalff (Bird and Kalff, 1986) and Shannon *et al.* (Shannon *et al.*, 2007), this algal group usually shows grazing rates comparable with those of HF. Many studies have demonstrated that mixotrophic algae are the major bacterial grazers in nutrient-poor systems, being responsible for >50% of the total bacterivory either in freshwater (Bird and Kalff, 1986; Domaizon *et al.*, 2003) or marine systems (Unrein *et al.*, 2007; Zubkov and Tarran, 2008). In particular, Jones (Jones, 2000) highlighted the importance of phagotrophic algae in humic lakes. According to Bergström *et al.* (Bergström *et al.*, 2003) the high allochthonous DOC concentration in humic systems promotes the growth of bacteria that are able to outcompete autotrophs for inorganic nutrients, rendering MF the dominant phytoplankters through the uptake of nutrients stored in bacterial biomass. These authors also observed that the MF:HF ratio was positively correlated to light availability, while Flöder *et al.* (Flöder *et al.*, 2006) experimentally demonstrated that even though cultures of *Ochromonas minima* (Chrysophyceae) were able to ingest bacteria under both high and low light conditions, they grew only under high light intensity. This suggests that photosynthesis can enable MF to outcompete heterotrophic ones during high light (midsummer) periods, and would explain the high MF:HF ratio observed in February in Rancho Hambre pools.

By analyzing the limnological parameters recorded over the same study period, González Garraza *et al.* (González Garraza *et al.*, 2012) found that all spring samples (October) were similar, and differed from most summer and autumn samples mainly on account of higher concentrations of dissolved oxygen, and lower concentrations of total phosphorus and nitrogen. Accordingly, all pools showed a similar structure of their plankton communities in spring (October, Fig. 6); with high abundances of early developmental stages of metazoans (MFN), the ciliates *H. grandinella* and large *Urotricha* sp., and low abundances of adult metazooplankton and HB. These results suggest that the plankton food webs from all pools were mainly driven by similar regulation pathways at the beginning of the open water period.

In late summer (February), the abundance of adult metazoan increased; yet small pools (RH3 and RH5) showed not only higher total abundances but also a different composition than large ones (RH1, RH2 and RH4) (Figs. 5 and 6). Small pools had higher abundances of predators and MFR than large ones, while abundances of MFN, OC and FC were noticeably lower. These differences in late summer metazooplankton structure could be partially explained by distinct water temperature variation patterns, as previous studies have demonstrated positive correlations between zooplankton features (survival, density and biomass) and temperature (Cook *et al.*, 2007; MacLennan *et al.*, 2012). In Rancho Hambre, not only was metazoan abundance positively correlated with water

temperature but also González Garraza *et al.* (González Garraza *et al.*, 2012) demonstrated the influence of pool size on the water temperature variations. Hence, the higher temperatures and wider diurnal variations in small, shallow pools (RH3 and RH5) would allow for maximum abundances of metazooplankton recorded in these pools (Fig. 5a).

Estimating carbon-based biomass values from abundance data allowed us to detect differences in the structure of the smaller plankton communities among spring and late summer, and also among large and small pools in the latter period. Not only did the C in the plankton biomass increase over the spring and summer in all pools, but also certain components (i.e. picoeukaryotes, AP, OC, FC and predators) accounted for more biomass in larger, deeper water bodies; while in shallow pools HB largely dominated the picoplankton, MF surpassed the AP and MFR represented most of the metazooplankton, strongly suggesting that energy is differently channeled through the trophic web in these two types of environments.

The framework proposed by the Gasol model (Gasol, 1994) allows potential trophic interactions to be inferred from abundance data. This model assumes that HF feed only on HB, that all HB are edible, and does not take into account other potential HB grazers. Although, as we discussed above, MF are important bacterial predators in Rancho Hambre, the first two assumptions of the model are met. Almost every HF found in the pools was <5 μm in size, which according to Sherr and Sherr (Sherr and Sherr, 1991) are the major bacteria predators within the size range of HF. In addition, picocyanobacteria were absent and picoeukaryotic algae were ~ 2 μm in size. Several studies have demonstrated that the HF from the size class 5–10 μm are the major grazers of 2 μm algae, whereas small HF (<5 μm in size) feed upon smaller prey (Sherr and Sherr, 1991; Sherr *et al.*, 1991), represented here by HB. Also, as discussed above, the lack of long bacterial filaments implies that at least as regards to size, all bacteria could be edible. The analysis of the two more distinct periods (October and February) according to the framework proposed by this model (Gasol, 1994) showed that HF abundance was mostly bottom-up regulated in spring samples; shifting to top-down control in all late summer samples. The degree of uncoupling between HB and HF abundances (D) for October and February pooled samples was positively correlated with the abundances of FC, predators, OC, MFR and the ciliate *P. fallax*, suggesting that all these could prey on HF. February samples showed high abundances of metazooplankton, dominated either by cladocerans in RH4 or rotifers in the rest of the pools. The negative impact of cladocerans on HF has been confirmed by several authors (Jürgens, 1994; Jürgens *et al.*, 1996; Tadonléké *et al.*, 2004; Sommer and Sommer, 2006); while rotifers caused a variation in the HB:HF relationship, probably through grazing on HF, both in unproductive (Tadonléké *et al.*, 2004) and productive (Fermani *et al.*, 2013) waters. The diet of the dominant OC *Boeckella poppei* Mrázek in turn, includes cells of 5 μm (Weller, 1977). The composition of mesozooplankton communities is known to be one important factor likely to regulate trophic interactions within the food web (Jürgens and Matz, 2002). In addition, the large ciliate *P. fallax* preys upon cells >2 μm (Šimek *et al.*, 1996). In this study, Gasol's model (Gasol, 1994) showed that, despite the fact that HF abundance does not vary appreciably among seasons or pool types, increases in the abundance of different metazoans and *P. fallax* would be key factors regulating their abundance in the different Rancho Hambre pools. Based on this evidence, we hypothesize that distinct changes in the trophic interactions along the entire food web of Rancho Hambre pools with different morphometrical features occur over the open water period, mainly on account of the temperature-driven changes in metazoan abundance, biomass and composition.

The present characterization of the spatial distribution, structure and temporal variation of the plankton communities along with the limnological characterization performed by González Garraza *et al.* (González Garraza *et al.*, 2012) constitute the first ecological baseline data for the complete plankton food web ever recorded from peat bog pools. Further experimental studies in Rancho Hambre as well as worldwide research of the plankton food web from peat bog pools will deepen our present insight into the structure and functioning of these unique environments by contributing to answer whether the space and time variation patterns found in the plankton communities of Rancho Hambre are representative of peat bogs worldwide and to what extent these systems differ from other humic environments.

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